Vision Research 51 (2011) 1117–1123

Contents lists available at ScienceDirect

Vision Research

journal homepage: www.elsevier.com/locate/visres

Asymmetries and idiosyncratic hot spots in crowding

Yury Petrov *, Olga Meleshkevich

Northeastern University, 125 NI, 360 Huntington Ave., Boston, MA 02115, USA

ARTICLE INFO

Article history:
Received 22 December 2010
Received in revised form 26 February 2011
Available online 23 March 2011

Keywords:
Psychophysics
Crowding

ABSTRACT

Crowding (mutual scrambling of nearby peripheral stimuli) has several known asymmetries. We explored these and other asymmetries systematically across the visual field. Crowding strength for 16 target (Gabor) positions in the visual field (8 directions × 2 eccentricities) were determined by positioning a plaid mask made of two transparently overlaid Gabors either inward, outward, clockwise, or counter-clockwise around the target. Overall, we found a surprisingly large individual variation in crowding strength appearing as idiosyncratic hotspots across the visual field. No correlations were found between the idiosyncratic variations of crowding and visual acuity either across the visual field or across subjects. When averaged across observers the results replicated most of the previously reported asymmetries of crowding. No new types of asymmetries were observed, but we found that the inward–outward asymmetry of crowding is present only along the horizontal meridian. Most surprisingly, we discovered that this asymmetry increases two-fold, if the observer is forced to attend to both left and right visual fields. This indicates that besides other factors attention allocation has a strong effect on the crowding asymmetry.

1. Introduction

Crowding is a ubiquitous and intriguing feature of spatial interactions in the periphery. Nearby visual items appear to scramble each other's appearance creating the crowding effect (e.g., Bouma, 1970, 1973; Levi, Klein, & Hariharan, 2002; Pelli, Palomares, & Majaj, 2004; Pelli, 2008; Stuart & Burian, 1962). In our recent study (Petrov, Popple, & McKee, 2007) we demonstrated that unlike surround suppression, crowding is strongly asymmetric: a mask outward of the target is on the average four times more disruptive than the same mask positioned inward, above or below. This peculiar property of crowding was first noticed by Bouma (1970) and has since been observed in numerous studies (e.g., Banks, Larson, & Prinzmetal, 1979; Bex, Dakin, & Simmers, 2003; Bouma, 1973; Chastain, 1982a, 1985; Krumhansl, 1977; Legge, Mansfield, & Chung, 2001; Wolford & Hollingsworth, 1974). Besides the inward–outward asymmetry crowding has other spatial asymmetries. Crowding is on the average stronger in the upper visual field (He, Cavanagh, & Intriligator, 1996), stronger along the radial direction (Toet & Levi, 1992), and, other factors taken into account, somewhat stronger for items arranged horizontally (Feng, Jiang, & He, 2007). Legge et al. (2001) also observed a weak tendency for letters positioned to the right within a string of letters to be less crowded than letters positioned to the left. The most pronounced of these other asymmetries is the radial-tangential effect, where crowding is 2–2.5 times stronger for items arranged along the radial (meridional) direction than along the tangential (isoeccentric) direction (Toet & Levi, 1992). Note that these asymmetries are not necessarily specific to crowding. In our recent study we demonstrated that, like crowding, surround suppression is significantly stronger in the radial direction (Petrov et al., 2007). On the contrary, the inward–outward asymmetry appears to be a distinctive property of crowding.

Because crowding appears to scramble visual features rather than suppress them, the current belief is that crowding results from some sort of spatial pooling happening in the peripheral vision (Pelli et al., 2004). The nature of this pooling is not known, and several different mechanisms were proposed. Flom, Weymouth, and Kahneman (1963) explained crowding by larger size of V1 receptive fields in the periphery, Levi, Klein, and Aitsebaomo (1985) – by larger size of V1 hypercolumns, Gilbert (1998) and Fitzpatrick (2000) attributed crowding to the effect of long-range horizontal connections, Neri and Levi (2006) – to imperfect co-registration of feature maps in the periphery. The common assumption of these explanations is that once features fall within the same receptive field (including its 'extra-classical' suppressive outskirts), the features interfere with each other and cannot be processed separately. Orbach and Wilson (1999), Parkes, Lund, Angelucci, Solomon, and Morgan (2001), Wilkinson, Wilson, and Ellemberg (1997) proposed higher-level mechanisms, such as some grouping process particularly active in the periphery, including texture formation or more general Gestalt-like grouping (Banks et al., 1979; Estes, Allmeyer, & Reder, 1976).

He et al. (1996) and Intriligator and Cavanagh (2001) explained crowding by a reduced spatial resolution of attention in the periphery, where features falling within the resolution 'spotlight' can not be individuated. Whether or not the 'spotlight' model of Posner,

* Corresponding author.
E-mail address: yury@neu.edu (Y. Petrov).

0042-6989/$ - see front matter © 2011 Elsevier Ltd. All rights reserved.
doi:10.1016/j.visres.2011.03.001

Snyder, and Davidson (1980), Eriksen and Yeh (1985), and Eriksen and St James (1986) describes allocation of spatial attention adequately is not particularly relevant here. There is accumulating behavioral (Belger & Banich, 1998; Liederman, 1998; Luck, Hillyard, Mangun, & Gazzaniga, 1989) and electrophysiological (Müller, Malinowski, Gruber, & Hillyard, 2003) evidence that attention can be applied independently to left and right hemifields, and can also be shaped into a doughnut (Müller & Hübner, 2002). So there might be two or more spotlights of complex shape, although the debate on this issue still continues (e.g., Jans, Peters, & De Weerd, 2010). Importantly, it appears that spatial attention cannot be focussed into a point or into the precise shape of the attended object, and crowding happens, when more than one object falls within the attended area.

It is important to investigate the crowding asymmetries, because such knowledge can be used to test the proposed mechanisms. For example, He et al. (1996) pointed out that crowding is weaker in the lower visual field, where attentional resolution is greater, which cannot be explained by the properties of V1 receptieve fields. Recently Dayan and Solomon (2010) suggested a quantitative model, where several paradoxical properties of crowding were successfully explained by optimal (Bayesian) inference operating over spatially extended receptive fields. In particular their model attempts to explain the inward–outward asymmetry of crowding based on the fact that the receptive field sizes increase with eccentricity. A conceptually similar hypothesis was proposed earlier by Motter and Simoni (2007).

Although the crowding asymmetries have been investigated in the several studies cited above, no study carried out its systematic exploration across the visual field. Bouma (1973), Wolford and Hollingsworth (1974), Krumhansl (1977), and Chastain (1982b, 1985) and other early studies positioned their stimuli along the horizontal meridian only. Toet and Levi (1992) investigated several target locations, but all were limited to one quadrant of the visual field. Only masks comprising two items positioned symmetrically across the target were used in their work. This made the crowding zone to appear artificially symmetrical. He et al. (1996) tested one position along the vertical meridian in the upper and lower visual fields. Legge et al. (2001) explored many target locations, but in the lower visual field only. Bex et al. (2003) used moving stimuli and averaged their results over many locations along the circular path. Feng et al. (2007) tested four target locations, one per quadrant of the visual field, but, the same as Toet and Levi (1992) used symmetric masks only.

The purpose of the present work was to study crowding asymmetries systematically across the visual field. We were particularly interested in the inward–outward asymmetry, which was never explored away from the horizontal meridian before.

2. Methods

2.1. Stimuli

The stimuli are shown in Fig. 1. The target was a standard cosine phase Gabor (a sinusoidal grating in cosine phase windowed by a two-dimensional Gaussian with spatial standard deviation $\sigma = \lambda/\sqrt{2}$) in which ~1.5 periods of the sinusoidal pattern were visible. The Gabor was slanted ±45° from the vertical; its contrast fixed at 45%. The plaid mask was made of two transparently overlaid Gabor patches. The patches were exact replicas of the target, except that one Gabor patch was rotated by 90°. Contrast of both patches was 45%; the resulting plaid contrast was close to 90%. The separation between the mask and the target centers was fixed at 4λ. The stimuli were displayed on a gray background and viewed on a linearized 21″ ViewSonic G225f monitor. The display resolution was set to 1600 × 1200 pixels, a pixel subtended ~1 min of arc.

2.2. Subjects

Six observers (3 males, 3 females, ages 26–38) with normal or corrected visual acuity were tested in the main experiment. Observers were trained for one or two experimental runs (10 min each) to get acquainted with the stimuli and the task. Observers viewed the stimuli binocularly while sitting 65 cm away from the screen. They were instructed to fixate at the fixation cross (shown in the center of the screen) at all times. Eye movements were not monitored, but we made sure that all the observers understood and remembered that keeping their fixation was critical for this study. All six subjects were experienced psychophysical observers and took part in similar experiments before, four of the observers were naïve to the purpose of the study. Testing lasted for several weeks, no significant learning effects were observed.

2.3. Psychometric procedure

The stimuli were presented at 16 tested locations in the visual field: 8 symmetric directions × 2 eccentricities (4° and 8°) shown in Fig. 2. For each location we tested four mask positions around the target defined with respect to fixation point: inward, outward, counter clockwise (CCW), and clockwise (CW), as shown in Figs. 1 and 2. Altogether, 16 × 5 conditions were tested in 16 blocks, the 16 target locations were blocked, the five mask conditions varied randomly within each block. The fifth mask condition actually had no mask in it and was used to measure the baseline performance for each target location. In each trial the target and mask simultaneously appeared at the tested location for 100 ms. In a 2AFC paradigm the observer had to identify the slant of the target (left or right) by pushing the left or right mouse button. A fixation cross was displayed at the center of the screen, and subjects were instructed to fixate at the cross for the whole duration of the trial.

To measure crowding, the Gabor period λ and, correspondingly, the target size, the mask size, and the target-mask separation, all varied according to the adaptive algorithm of Kontsevich and Tyler (1999), until observers were unable to perform the task, which determined a threshold stimulus size. This approach is similar to the "critical spacing" method, the only difference is that here the target and mask sizes vary proportionally to the target-mask separation. This procedure has the advantage of precluding the mask overlapping the target, which was a concern for our study: because

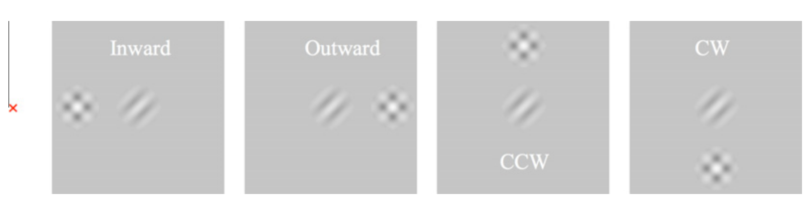

Fig. 1. Experimental stimuli were comprised of a Gabor target and a plaid mask. The target appeared in one of 16 possible positions in the visual field (8 directions × 2 eccentricities). The target is shown in the 3 o'clock position with respect to the fixation cross (indicated schematically on the left). The masks are in the four positions used for the study.

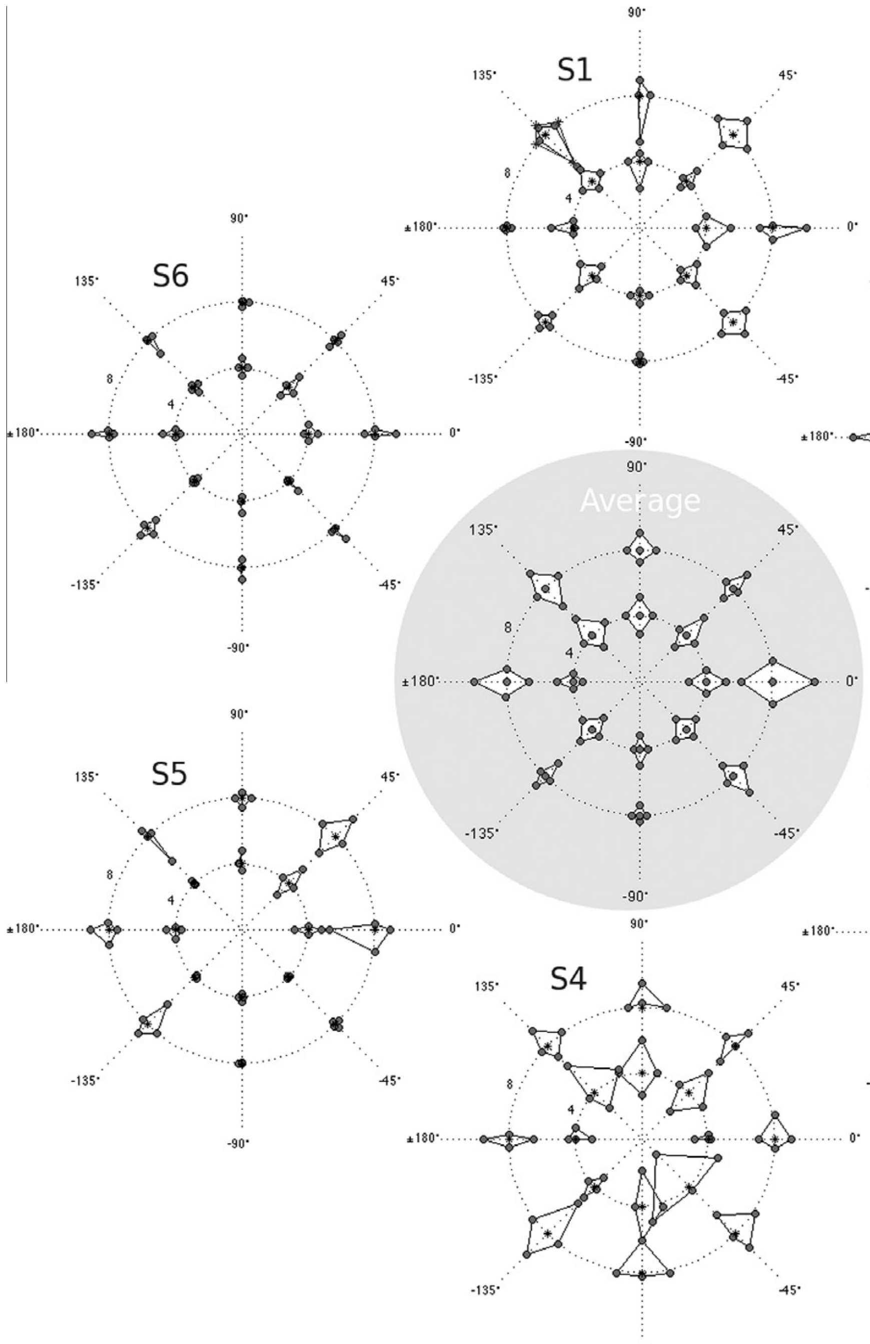

Fig. 2. Crowding factor as a function of the target location in the visual field and the mask location around the target. Each subplot displays an individual subject's data, the central subplot shows the averaged data. The tested target positions are indicated by the asterisks. For each position and each mask location around the target the corresponding crowding factor is indicated by a red disk, the disk's separation from the target is proportional to the crowding factor. The disks were joined to better illustrate the asymmetry of crowding. Note that the shapes reflect the asymmetry of the crowding strength rather than the shape and extent of the crowding zone. Four months later observer S1 repeated the experiment for one target location; these control results shown in blue are overlaid on the original data.

we used a single mask, crowding was weak for some subjects, and such overlap would have happened otherwise. Instead of using the "critical spacing" we measured crowding in terms of a crowding factor defined as the ratio of the masked to unmasked size thresholds (λs) minus 1. Zero factor corresponded to no crowding. Thus, we measured crowding strength instead of crowding extent, but these two measures are, clearly, positively correlated. Both thresholds were measured within the same experimental session to minimize variation of results due to performance fluctuations. The unmasked thresholds reflect subjects' visual acuity, they varied among subjects from 6.8 cpd to 14.5 cpd for 8° eccentricity targets, and from 6.8 cpd to 17.8 cpd for 4° eccentricity targets (Fig. 3). Observers carried out three blocks of 50 trials per block for each condition. Uncertainties of the psychometric thresholds were taken as the maximum of the two: (i) threshold variation calculated from the results of the adaptive algorithm, (ii) threshold variation in between the three experimental blocks.

3. Results and discussion

The full experimental data for six observers are shown in Fig. 2. The results averaged over the visual field and analyzed for various

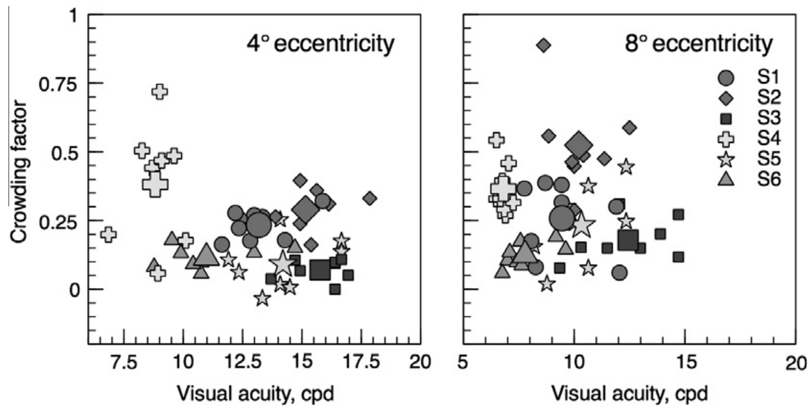

Fig. 3. Testing correlation between visual acuity and crowding. Visual acuity and crowding factor were plotted along x and y axes respectively. Disks represent an individual subject's data for a given target location averaged over the four mask locations around the target. Stars show data for each subject averaged over all (8) locations. The left and right panels show data for 4° and 8° target locations respectively.

symmetries of the crowding zone are shown in Fig. 4. Results in Fig. 2 are presented as a polar plot representing the visual field. The asterisks mark the 16 tested target locations. The red disks indicate the mask directions: inward, outward, clockwise, and counter clockwise with respect to each target location. Distances between asterisks and red circles are proportional to the corresponding crowding factors. Solid black lines are mere guides to the eye and roughly illustrate the asymmetry of crowding at each location. While this representation allows to show the crowding asymmetry succinctly, it should not be confused with crowding zones: the diamond shapes in Fig. 2 reflect crowding strength asymmetry, not the corresponding crowding zones.

There was a surprisingly large variation in the overall strength of crowding among subjects (Fig. 2). In addition, crowding appears to form idiosyncratic hotspots: crowding factors varied across the visual field in a haphazard fashion for all subjects. For example, S1 demonstrated strong crowding along the vertical meridian in the upper visual field. Strikingly, crowding had inward asymmetry at both 4° and 8° eccentricities along this meridian: the inward mask crowded five times stronger than the outward mask. The same applies to the next target location counter clockwise. This is in the opposite direction from the conventional outward asymmetry of crowding observed for the same subject along the horizontal meridian. Note that the observed large variation does not result from poor statistics or inconsistent performance. With an interval of four months S1 repeated the experiment for one target location, and the new results shown in blue in Fig. 2 were nearly identical to the old ones.

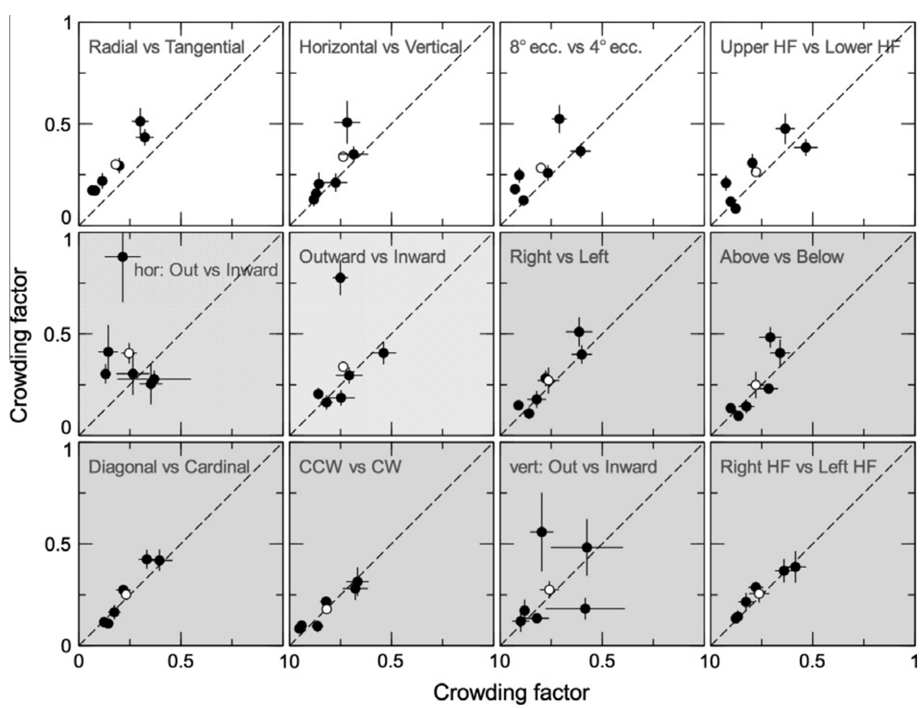

Fig. 4. Tests for various asymmetries of crowding. Crowding factor was plotted along x and y axes in each subplot. Each black disk represents an individual subject's data averaged across the visual field over the target-mask configurations which conformed with the tested type of symmetry. For example, for the "Radial vs. Tangential" subplot all radial mask crowding factors (inward and outward × 16 target locations = 32 altogether) and all tangential mask crowding factors (CW and CCW × 16 target locations = 32 altogether) in Fig. 2 were averaged. The white disks display the subjects average. Error bars indicate one standard deviation. The shaded subplots display the results for which no statistically significant asymmetries were observed.

The inter-subject variation of crowding can not be explained by variations in visual acuity among subjects. Fig. 3 shows crowding factor correlated with visual acuity for each subject and for each tested target location. The crowding factors averaged over the four mask positions around each target location are plotted along the *y*-axis. Visual acuity measured as the target-alone cpd thresholds for left/right orientation discrimination are plotted along the *x*-axis. Altogether, there was no significant correlation between acuity and crowding across the visual field for each individual subject (disks of the same color). For example, S4 had very stable acuity thresholds for each eccentricity but large variation in crowding strength. S3, on the opposite, had large variation in acuity but small variation in crowding. Similarly, there was no significant correlation between acuity and crowding across subjects (subject means are shown by stars).

Because of the large inter-subject variation it is difficult to perceive any common crowding features in individual data in Fig. 2. The central subplot shows data averaged over subjects. On the averaged plot some features of crowding become more apparent. Crowding was stronger at 8° than at 4° eccentricity. There was a pronounced radial-tangential asymmetry, which can be seen as the elongation of the diamond shapes in the radial direction. There was also a somewhat larger elongation in the outward direction along the horizontal meridian, which reflects the inward–outward asymmetry of crowding along this meridian. Crowding was stronger in the upper visual field.

To probe the symmetries of crowding in a different fashion we averaged the data over the visual field instead of averaging it over the observers (Fig. 4). Each subplot shows the results of averaging over all the target-mask configurations which conform to a given type of symmetry. For example, the data plotted along the *y*-axis of the first subplot (radial) were averaged over all 16 target locations and also over the two radial mask positions (inward and outward). For the *x*-axis (tangential) all clockwise and counterclockwise data were averaged instead. Individual subject's data are shown by black disks, averaged data – by white disks. A crowding asymmetry appears as a deviation of the corresponding average away from the diagonal in this format. Asymmetry was deemed significant, if the subjects average was more than two standard deviations away from the diagonal. The significance is indicated in subplots of Fig. 4 by white background; subplots with insignificant effects have shaded backgrounds.

Overall, the significant features of crowding were in agreement with crowding asymmetries found in previous studies. Radial masks, horizontally arranged masks, and masks positioned outward of the target produced stronger crowding. Crowding was also stronger at larger eccentricities, and in the upper visual field. All the rest of the tested asymmetries, including the outward mask vs. inward mask along the vertical meridian, diagonal vs. cardinal direction mask, and above vs. below mask were insignificant.

We found a tendency for stronger crowding from a mask positioned to the right compared to a mask positioned to the left of the target, which was earlier observed by Legge et al. (2001), but this asymmetry was not statistically significant for our data. Bouma (1973) found a stronger crowding in the left visual field. If anything, we observed a slightly stronger crowding in the right visual field. However, this effect was insignificant.

The inward–outward asymmetry along the horizontal meridian and also when averaged across the whole visual field was statistically significant, but only due to the very pronounced effect for observer S2. Therefore, we left the corresponding panels in Fig. 4 partially shaded. Note, that all the previous studies where the inward–outward asymmetry of crowding was observed restricted their stimuli to the horizontal meridian (Banks et al., 1979; Bouma, 1973; Chastain, 1982b, 1985; Krumhansl, 1977; Petrov et al., 2007; Petrov & Meleshkevich, 2011; Petrov & Popple, 2007; Wolford & Hollingsworth, 1974) or averaged data over multiple stimulus locations (Bex et al., 2003; Legge et al., 2001). Our results indicate that the asymmetry may be specific to the horizontal meridian only.

Although the inward–outward asymmetry of crowding was significant along the horizontal meridian, it was much weaker than expected based on the previous studies, including our own. In these studies the outward mask produced 3–4 times stronger crowding than the inward mask (Bex et al., 2003; Legge et al., 2001; Petrov & Meleshkevich, 2011; Petrov & Popple, 2007; Petrov et al., 2007). In the present experiment this outward–inward factor was only 1.6. In fact, this factor was not significantly different from 1 for half of the observers. The most obvious difference of the present study was that the location of the stimulus was fixed for each run, so that subjects could focus their attention entirely onto the one given location. In our earlier studies two stimulus locations were used, left and right of fixation, and, therefore, subjects had to divide their attention between left and right visual fields. The same applies to all the studies in which strong inward–outward asymmetry was observed (Bex et al., 2003; Bouma, 1973; Chastain, 1982b, 1985; Krumhansl, 1977; Legge et al., 2001; Wolford & Hollingsworth, 1974). Banks et al. (1979) used stimuli consisting of the target and mask letters fixed in either left or right visual field and, similarly to our present study, found only weak inward–outward asymmetry. The only exception is our own study, where a triplet of Gabor targets positioned along the horizontal meridian (always in the same visual field) had to be identified. Subjects made very few errors identifying the orientation of the outmost Gabor compared to the remaining two targets (Petrov & Popple, 2007). However, to do this task the attention had to be spread over the whole triplet, and it is possible that such a spread, similarly to splitting attention between left and right visual fields, resulted in the strong outward-inward asymmetry. Because we did not monitor eye movements, there remains a possibility that observers, although experienced and instructed to fixate at all times, made involuntary micro saccades or slightly shifted their fixation in the direction of the stimulus. It is not clear how such small gaze shifts could produce the observed weakening of the inward–outward asymmetry, and we find the attentional explanation more likely.

To test the hypothesis that simultaneous attention to left and right visual fields increases the inward–outward asymmetry of crowding we ran a control experiment. The stimuli were simultaneously presented at two symmetric locations 8° left and right of a fixation point, and the task was to identify the location, where the target Gabor was slanted to the left. The rest of the experimental parameters and procedures were identical to the main experiment. All subjects except S2 participated in this experiment. We observed a large increase of crowding from the outward mask, while crowding from the inward mask did not change, as shown in Fig. 5. Also, variation of the outward mask crowding among subjects increased quite dramatically. In the same figure we plotted data for four additional subjects (shown with black diamonds), which participated in this experiment as a part of a different study. The average ratio of the crowding factors for outward and inward masks was more than 3:1; this value was in agreement with our previous studies and twice as large as obtained in the main experiment. The result of the control experiment confirms that the mode of attention allocation strongly modifies the crowding asymmetry.

3.1. General discussion

The findings of this study are two-fold. First, the crowding strength varied quite dramatically among observers. Besides, for each observer it varied strongly as a function of the target location in the visual field as well as the mask location with respect to the target. It is important to note that the strong inter-subject variation

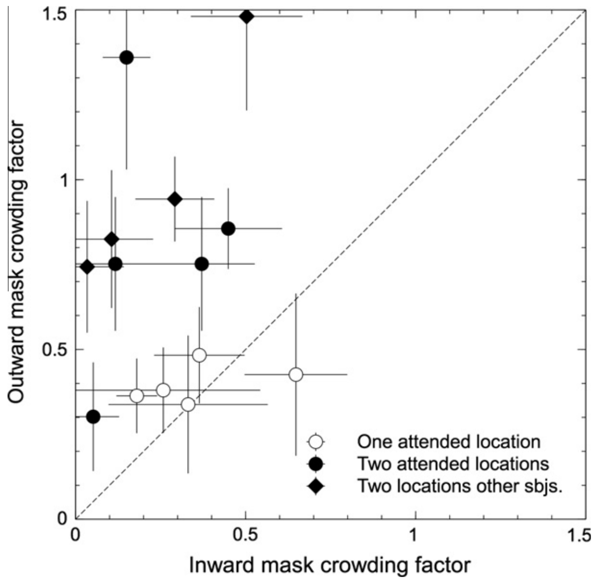

Fig. 5. The effect of attention allocation on the inward–outward asymmetry of crowding. The crowding factors for inward mask and outward mask are plotted along the *x* and *y* axes respectively. The white disks show individual subjects data for the the main experiment, where the target positions 8° left and right of fixation were tested in separate runs. The black disks show data for the same observers, where the two target locations were randomly interleaved within the same experimental run. The black diamonds show data for additional subjects.

does not contradict earlier reports and is not an artefact of statistical noise or the particular methods that we used here. Similarly strong variation was observed (but not necessarily emphasized) in all other crowding studies, where a large number of subjects was used and individual data were shown (Feng et al., 2007; Kooi, Toet, Tripathy, & Levi, 1994; Legge et al., 2001; Petrov & Meleshkevich, 2011; Petrov et al., 2007; Toet & Levi, 1992). This fact was mentioned in the recent review by Pelli (2008), but it appears to be commonly overlooked. In particular, it necessitates testing many subjects for any crowding study. Despite the strong inter-subject variation, several crowding asymmetries were apparent for most subjects, and were statistically significant for the individual and averaged data. Crowding was stronger for radial mask than for tangential mask, stronger for horizontal mask than for vertical mask, stronger in the periphery than in the parafovea, stronger in the upper visual field. These results agree with the crowding asymmetries reported earlier in separate studies (Bouma, 1970; Feng et al., 2007; He et al., 1996; Toet & Levi, 1992). The new finding in our study is that the variation of the crowding strength across subjects and across the visual field for each subject does not correlate with the subject's visual acuity at a given location. This fact argues against explaining crowding by some low-level mechanism (e.g., the receptive field sizes in V1 as in Flom et al. (1963) and Levi et al. (1985)), because in this case one would expect crowding and acuity to be correlated.

Second, we found that the strong inward–outward asymmetry observed in many earlier studies was limited to the horizontal meridian of the visual field, and even along this meridian it was rather weak unless the subject's attention was directed to target locations in both visual hemifields. The inward–outward asymmetry increased about two-fold then. The strong effect of attention allocation is in line with several recent studies Põder (2006, 2007), Yeshurun and Rashal (2010) and our recent study, where we observed that the inward–outward asymmetry can be dramatically reduced or even reversed by manipulating attention (Petrov & Meleshkevich, 2011). Yeshurun and Rashal (2010) showed that crowding zone was reduced, when attention was cued to a known location in one hemifield compared to being split between two hemifields. This agrees with the results of our control experiment. We showed, more specifically, that focusing attention to one hemifield reduces outward crowding but leaves inward crowding unaffected. Põder (2006, 2007) demonstrated that salience-based, i.e., exogenously controlled attention reduced crowding as well as the endogenously controlled attention in our study. More to the point, (Petrov & Meleshkevich, 2011) showed that attention allocation *per se* is biased outward along the horizontal meridian, which suggests that the crowding asymmetry results from the attentional bias, which links crowding to attention in a very specific way. It is unclear what makes the horizontal meridian special (predominant text orientation, maybe), what biases attention outward along this meridian, and why this bias is stronger, when attention is split between two visual hemifields. Although it is clear that the strong effect of attention lends some support to the insufficient attentional resolution mechanism of crowding (He et al., 1996; Intriligator & Cavanagh, 2001), it is also possible that attention simply plays a facilitatory role, as suggested by Põder (2006), Yeshurun and Rashal (2010), Mareschal, Morgan, and Solomon (2010): attending to the target increases its weight with respect to the mask and makes the target better represented after the pooling stage in crowding. Conversely, when the mask is attended, crowding intensifies. In this scenario the distribution of attention between target and mask modulates crowding, but some other factor, not necessarily attention, causes the actual pooling.

3.2. Conclusion

In this study we explored the distribution of crowding across the visual field. Crowding varied strongly among observers both in terms of its overall strength and in terms of its spatial asymmetry. The crowding strength varied significantly across the visual field for each observer; there were distinct hotspots, where crowding was much stronger than elsewhere. Once the results were averaged among observers, the asymmetries of crowding known from earlier studies were revealed. When averaged across observers the inward–outward asymmetry of crowding was found along the horizontal but not along the vertical meridian. This asymmetry was strongly modulated by the mode of attention allocation: splitting attention between left and right visual fields increased the asymmetry two-fold.

Acknowledgment

We would like to thank Dr. Suzanne McKee and Dr. Ariella Popple for helpful discussions.

References

Banks, W. P., Larson, D. W., & Prinzmetal, W. (1979). Asymmetry of visual interference. *Perception and Psychophysics, 25*(6), 447–456.
Belger, A., & Banich, M. T. (1998). Costs and benefits of integrating information between the cerebral hemispheres: A computational perspective. *Neuropsychology, 12*(3), 380–398.
Bex, P. J., Dakin, S. C., & Simmers, A. J. (2003). The shape and size of crowding for moving targets. *Vision Research, 43*(27). 2895-904. 16.
Bouma, H. (1970). Interaction effects in parafoveal letter recognition. *Nature, 226*(5241), 177–178.
Bouma, H. (1973). Visual interference in the parafoveal recognition of initial and final letters of words. *Vision Research, 13*(4), 767–782.
Chastain, G. (1982a). Feature mislocalizations and misjudgments of intercharacter distance. *Psychological Research, 44*(1), 51–65.
Chastain, G. (1982b). Masking and the identification of characters presented simultaneously and sequentially to the parafovea. *Psychological Research, 44*(2), 135–145.
Chastain, G. (1985). Positional differences in performance on members of confusable and nonconfusable letter pairs. *Journal of Experimental Psychology: Human Perception and Performance, 11*(6), 752–764.
Dayan, P., & Solomon, J. A. (2010). Selective bayes: Attentional load and crowding. *Vision Research, 50*(22), 2248–2260.

Eriksen, C. W., & St. James, J. D. (1986). Visual attention within and around the field of focal attention: A zoom lens model. *Perception and Psychophysics, 40*(4), 225–240.

Eriksen, C. W., & Yeh, Y. Y. (1985). Allocation of attention in the visual field. *Journal of Experimental Psychology: Human Perception and Performance, 11*(5), 583–597.

Estes, W., Allmeyer, D., & Reder, S. (1976). Serial position functions for letter identification at brief and extended exposure durations. *Perception and Psychophysics, 19*(1), 1–15.

Feng, C., Jiang, Y., & He, S. (2007). Horizontal and vertical asymmetry in visual spatial crowding effects. *Journal of Vision, 7*(2), 13.

Fitzpatrick, D. (2000). Seeing beyond the receptive field in primary visual cortex. *Current Opinion in Neurobiology, 10*(4), 438–443.

Flom, M. C., Weymouth, F. W., & Kahneman, D. (1963). Visual resolution and contour interaction. *Journal of the Optical Society of America, 53*, 1026–1032.

Gilbert, C. (1998). Adult cortical dynamics. *Physiological Reviews, 78*(2), 467–485.

He, S., Cavanagh, P., & Intriligator, J. (1996). Attentional resolution and the locus of visual awareness. *Nature, 383*(6598), 334–337.

Intriligator, J., & Cavanagh, P. (2001). The spatial resolution of visual attention. *Cognitive Psychology, 43*(3), 171–216.

Jans, B., Peters, J. C., & De Weerd, P. (2010). Visual spatial attention to multiple locations at once: The jury is still out. *Psychological Review, 117*(2), 637–684.

Kontsevich, L. L., & Tyler, C. W. (1999). Bayesian adaptive estimation of psychometric slope and threshold. *Vision Research, 39*(16), 2729–2737.

Kooi, F. L., Toet, A., Tripathy, S. P., & Levi, D. M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spatial Vision, 8*(2), 255–279.

Krumhansl, C. L. (1977). Naming and locating simultaneously and sequentially presented letters. *Perception and Psychophysics, 22*(3), 293–302.

Legge, G. E., Mansfield, J. S., & Chung, S. T. (2001). Psychophysics of reading. xx. linking letter recognition to reading speed in central and peripheral vision. *Vision Research, 41*(6), 725–743.

Levi, D. M., Klein, S. A., & Aitsebaomo, A. P. (1985). Vernier acuity, crowding and cortical magnification. *Vision Research, 25*(7), 963–977.

Levi, D. M., Klein, S. A., & Hariharan, S. (2002). Suppressive and facilitatory spatial interactions in foveal vision: foveal crowding is simple contrast masking. *Journal of Vision, 2*(2), 140–166.

Liederman, J. (1998). The dynamics of interhemispheric collaboration and hemispheric control. *Brain and Cognition, 36*(2), 193–208.

Luck, S. J., Hillyard, S. A., Mangun, G. R., & Gazzaniga, M. S. (1989). Independent hemispheric attentional systems mediate visual search in split-brain patients. *Nature, 342*(6249), 543–545.

Mareschal, I., Morgan, M. J., & Solomon, J. A. (2010). Attentional modulation of crowding. *Vision Research, 50*(8), 805–809.

Motter, B. C., & Simoni, D. A. (2007). The roles of cortical image separation and size in active visual search performance. *Journal of Vision, 7*(2), 6.1–6.15.

Müller, M., & Hübner, R. (2002). Can the spotlight of attention be shaped like a doughnut? Evidence from steady-state visual evoked potentials. *Psychological Science, 13*(2), 119.

Müller, M. M., Malinowski, P., Gruber, T., & Hillyard, S. A. (2003). Sustained division of the attentional spotlight. *Nature, 424*(6946), 309–312.

Neri, P., & Levi, D. M. (2006). Spatial resolution for feature binding is impaired in peripheral and amblyopic vision. *Journal of Neurophysiology, 96*(1), 142–153.

Orbach, H. S., & Wilson, H. R. (1999). Factors limiting peripheral pattern discrimination. *Spatial Vision, 12*(1), 83–106.

Parkes, L., Lund, J., Angelucci, A., Solomon, J. A., & Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nature Neuroscience, 4*(7), 739–744.

Pelli, D. G. (2008). Crowding: a cortical constraint on object recognition. *Current Opinion in Neurobiology, 18*(4), 445–451.

Pelli, D. G., Palomares, M., & Majaj, N. J. (2004). Crowding is unlike ordinary masking: distinguishing feature integration from detection. *Journal of Vision, 4*(12), 1136–1169.

Petrov, Y., & Meleshkevich, O. (2011). Locus of spatial attention determines inward–outward anisotropy in crowding. *Journal of Vision*, in press.

Petrov, Y., & Popple, A. V. (2007). Crowding is directed to the fovea and preserves only feature contrast. *Journal of Vision, 7*(2), 8.1–8.9.

Petrov, Y., Popple, A. V., & McKee, S. P. (2007). Crowding and surround suppression: Not to be confused. *Journal of Vision, 7*(2), 12.1–12.9.

Põder, E. (2006). Crowding, feature integration, and two kinds of "attention". *Journal of Vision, 6*(2), 163–169.

Põder, E. (2007). Effect of colour pop-out on the recognition of letters in crowding conditions. *Psychological Research, 71*(6), 641–645.

Posner, M. I., Snyder, C. R., & Davidson, B. J. (1980). Attention and the detection of signals. *Journal of Experimental Psychology, 109*(2), 160–174.

Stuart, J. A., & Burian, H. M. (1962). A study of separation difficulty. Its relationship to visual acuity in normal and amblyopic eyes. *American Journal of Ophthalmology, 53*, 471–477.

Toet, A., & Levi, D. M. (1992). The two-dimensional shape of spatial interaction zones in the parafovea. *Vision Research, 32*(7), 1349–1357.

Wilkinson, F., Wilson, H. R., & Ellemberg, D. (1997). Lateral interactions in peripherally viewed texture arrays. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 14*(9), 2057–2068.

Wolford, G., & Hollingsworth, S. (1974). Retinal location and string position as important variables in visual information processing. *Perception and Psychophysics, 16*(3), 437–442.

Yeshurun, Y., & Rashal, E. (2010). Precueing attention to the target location diminishes crowding and reduces the critical distance. *Journal of Vision, 10*(10), 16.